# Aspects of Ctenidial Feeding in Immature Bivalves

BY

CHARLES R. STASEK

Friday Harbor Laboratories, University of Washington, Seattle, and Stazione Zoologica, Naples, Italy

(2 Textfigures)

## *Introduction*

The margins of the two gills, or ctenidia, of most adult bivalved mollusks are grooved. The grooves are ciliated and function in the transfer to the mouth of potential food particles that the ctenidia filtered from the so-called respiratory water current. The suggestion has been made and accepted in the literature that the ctenidia of developing bivalves cannot function in this way until the marginal food grooves make their appearance (Yonge, 1947; Allen, 1961). The acceptance of this suggestion as a "fact" is premature, for the limited observations related below have proved it to be untrue.

## *Observations*

The adult ctenidia of Modiolaria laevigata Gray are similar in cross-section to those of Mytilus; that is, each is "W"-shaped with a food groove along the margin of each "V", or demibranch (see Atkins, 1937, p. 383). Of one specimen of Modiolaria only 1.9 mm. greatest dimension, 21 ctenidial filaments had formed on either side of the body. Of those on the right side, the 13 nearest the mouth consisted solely of descending and ascending filaments of the inner demibranch. The remaining 8 filaments bore rudiments of the descending arm of the outer demibranch (Fig. 1). Despite the facts that there was neither a food groove on the inner demibranch nor a "complete" outer demibranch, ciliary currents along all free margins, including that of the unreflexed outer demibranch, carried particles towards the mouth. In the young as in the adult there is also a strong ciliary tract in the axis of the ctenidium between the demibranchs. If in Modiolaria the development of these earlier filaments is like that of Mytilus, the short papillae comprising the descending arm of the outer demibranch will continue to grow downwards and then bend back upon themselves leading to the completed "W"-shape of the adult ctenidium.

Cross-sections of the right ctenidium of Venericardia ventricosa Gould (Carditidae) at three stages of development are shown in Figure 2. The inner demibranch develops before the outer, with orally directed tracts of cilia being present along its margin even in the absence of a food groove (Fig. 2A). The ctenidium passes through a stage, when the animal is about 3.1 mm. greatest dimension, in which the outer demibranch is represented by small reflexed filaments that seem to lack orally directed tracts along their margins (Fig. 2B); ciliary tracts lead particles over the margin of the outer demibranch into the axis of the ctenidium where a strong tract persisting from younger stages leads them towards the mouth. A shallow food groove is present on the inner demibranch (MGI). The only available specimen in this size range died before the existence of orally directed

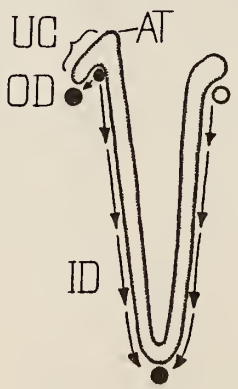


Figure 1: Diagrammatic cross-section of the ctenidium of *Modiolaria* at an early stage of development.
AT: area of attachment of ctenidium to body
ID: inner demibranch
OD: outer demibranch
UC: unciliated abfrontal surface of outer demibranch
• : strong orally directed currents
o : weaker orally directed currents
Arrows indicate direction of beat of frontal cilia

tracts along the edges of the reflexed segments could be ascertained, but such are probably present.

At 4.9 mm. greatest dimension this species has well-developed food grooves on the inner demibranchs and weak, orally directed tracts on the ungrooved margins of the outer demibranchs (Fig. 2 C). Approximately the upper half of the ascending filaments bears frontal ciliation beating towards the reflexed edge. The proportion of the length of the reflexed portions of the outer filaments given to this type of frontal ciliation becomes somewhat larger as the organism grows, but the general arrangement is similar to that of adults of 18 mm. greatest dimension.

Although Venericardia is eulamellibranchiate when adult, interfilamentary junctions of the ctenidium seem to be entirely ciliary at very early stages.

## *Conclusions*

The inner demibranchs of Modiolaria and Venericardia are functional, food-collecting organs before the outer demibranchs commence their development. It is probably characteristic of all bivalves that elements of the inner demibranchs appear before those of the outer (Rice, 1908; Creek, 1960). While the amount of water passing over their surfaces is no doubt small, the outer demibranchs from their first appearance seem to be food-collecting structures. The ctenidial axis will probably be found to be significant in leading particles to the mouth.

At a stage intermediate in development (Fig. 2 B), a cross-section of the ctenidium of Venericardia bears some resemblance to that of adult Cardiidae (see Johnstone, 1900), although that family lacks the orally directed tracts along the reflexed margins of the ctenidia.

The arrangement of the frontal ciliation of Venericardia ventricosa is unique among known bivalves. The division of frontal ciliation on the ascending lamellae of the outer demibranchs recalls that of the Unionidae (Atkins, 1937, p. 408), but that family lacks orally directed tracts on the margins of the outer demibranchs and of the reflexed margins of the inner ones.

While there are structural and functional differences between the organs and methods of feeding of young and adult bivalves (see Allen, 1961), the general rôle of food collection probably may be attributed to the ctenidia shortly after their first appearance. Their function cannot be deduced from form alone.

## *Acknowledgment*

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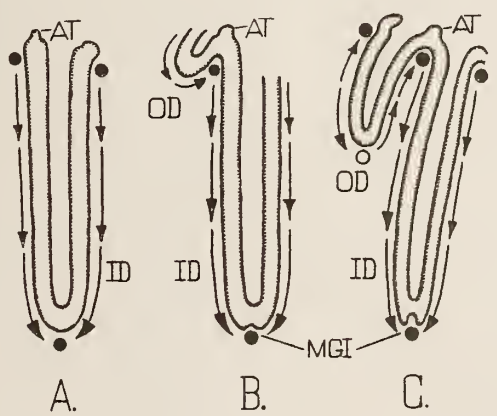


Figure 2: Diagrammatic cross-sections of the ctenidium of *Venericardia* at three stages of development.
MGI: marginal food groove
Other abbreviations as in Figure 1

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